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**ORIGINS OF THE FAUNA OF THE SITKAN DISTRICT,
ALASKA***

BY

HARRY S. SWARTH

*Late Curator, Department of Ornithology and Mammalogy
California Academy of Sciences*

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INTRODUCTION

Islands and mainland of extreme southeastern Alaska comprise a sharply defined geographic area set off by natural boundaries that coincide closely with present day political lines. The region possesses bird and mammal populations, as well as plants, that are sufficiently characteristic to justify the distinctive name "Sitkan district" that has been applied by biologists to this part of Alaska (see Nelson, 1887, p. 24). The natural history of the country has been studied enough and from sufficiently extensive collections to warrant some general conclusions regarding origins of the animal life. My own personal experience includes field work that has covered most of the Sitkan district and some of the coast to the southward, as well as additional seasons spent in the immediately adjoining interior of Yukon Territory and British Columbia. It is,

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I think, the background of actual field experience that is responsible for most of the personal opinions and theories that are here expressed. Conditions east of the Coast Range are touched upon lightly and incidentally in this discussion, but it is surprising to how great an extent field work east of those mountains has supplied clues to the solution of problems concerning the very different fauna west of the range.

In any given region some proportion of the species may be recognized more or less plainly as immigrants from elsewhere, but there are not many places sharply circumscribed as is the Sitkan district where the facts regarding immediate origins are so plainly indicated in such a large number of cases, and where so many rather striking deductions and inferences follow even limited comprehension of observed facts. Not that the whole story is presented here by any means, even of the representative species to which this discussion is confined. There is much that remains obscure in the local distribution of forms. Each species has its own history, with details varying from those of all the others, though in general agreement with some one of the several categories of immigrants that may be recognized. Then, while our knowledge of species and conditions is reasonably satisfactory, there is no doubt that further field work in the region would add much, especially in information about the small mammals. Furthermore, the mainland coast of British Columbia is practically unexplored as regards its fauna, and while this is of lesser concern so far as birds are concerned, it is of extreme importance with the mammals. The stretch of coast line extending southward from the Alaska boundary unquestionably holds valuable information bearing upon the Alaskan species.

PHYSIOGRAPHICAL FEATURES OF THE SITKAN DISTRICT

The Sitkan district, Alaska, as here defined, includes the Alaska "pan-handle," namely, a narrow strip of mainland coast west from the summit of the Coast Range, from Glacier Bay at the north, south to Dixon Entrance, together with the adjacent islands, the Alexander Archipelago. The region described has been more recently glaciated than any other section of North America. "The great cordilleran ice sheet of northwestern America, which, according to Dawson, swept north and south from its source in British Columbia, probably only reached into southeastern Alaska, where it passed through the coast range gaps, and, uniting with the local glaciers from these mountains, helped to scour out the extensive system of waterways of the Pacific shore and covered a good part of the Alexander Archipelago. The evidence of glacial erosion in this southeastern province indicates a great thickness of ice, and here, unlike other parts of Alaska, the ice overrode considerable altitudes. The large unmapped areas in the islands make it impossible to indicate the limits of the ice sheet, but it probably covered most of the

archipelago¹ and dumped its debris directly into the Pacific beyond" (Brooks, 1906, p. 246). Dawson (1888, p. 347) also says "The glacier extending from the mainland coast touched the northern shores of the Queen Charlotte Islands"; and (*op. cit.*, p. 348) "The front of the glacier must have passed the outer border of the Archipelago, as at Sitka well-marked glaciation is found pointing toward the open Pacific." (See also F. E. and C. W. Wright, 1908, pp. 27, 77.) It should be borne in mind, too, that "The glaciation of Alaska is to be regarded rather as an extension of the present system of alpine and piedmont glaciers than as a continental ice sheet. . . . The older glacial system was, however, far more extensive, and in southeastern Alaska approached the continental type" (Brooks, 1906, p. 245).

In general, the Pleistocene is regarded as including the last epoch of extensive glaciation, but, clearly, much of southeastern Alaska must have remained ice covered after the close of that period. This region now contains the most extensive glaciers in North America, glaciers that have changed enough during the few years that they have been under observation to suggest enormously greater expanse even a few hundred years ago. Publications on this subject written by various individuals convey more than an implication of this belief (see Wright, 1887, pp. 250-256). The one dissenting account that I have seen (Capps, 1915) deals with the White River Basin, Wrangell Mountains, about at the northern limit of glaciation in this part of Alaska, and it is not clear that the author's conclusions regarding conditions at this inland station are applicable to the coast. He places the period of glacial retreat at that point as far back as 8,000 years.

From the foregoing discussion it would seem that the post-glacial reoccupation of southeastern Alaska by animal and plant life must have been at a more recent date than was the case in any other as extensive area in temperate North America. The inescapable and important conclusion is that whatever is peculiar to the Sitkan fauna and flora must inevitably have developed subsequent to Pleistocene time. Avian paleontologists have lately been expressing more and more definitely their conviction that many present day forms are of greater age than this, that modern genera were in existence in large part in the Miocene, some of them still earlier. "In the Miocene. . . . appear birds so closely allied to our modern species that in many cases they may be assigned to living genera." "When the avifauna of the Ice Age and of the latter part of the Tertiary is better known we shall unquestionably find it much richer in species than is the case in present times since the greater part, if not all of our modern forms, were in existence contemporaneously with many peculiar birds that have become extinct" (Wetmore, 1927, pp. 182, 183). Paleontological evidence deals with structural characters, necessarily. In the Sitkan fauna we seem to be supplied with evidence

¹ Not, however, the highest summits. H. S. S.

bearing upon the age of such external characters as color and pattern. Here we have a number of strongly characterized forms (mostly "subspecies," though there are some that we call species) that show a common tendency to vary in the same direction, and that have developed subsequent to the Pleistocene. It seems, therefore, that in the Sitkan district, Alaska, considered in contrast with adjacent regions, the present day fauna and flora afford excellent subject matter for speculation upon species formation. There are not many regions where we can assume, as here, so nearly exact and so recent a date for the inception of its animal life. From the adjacent interior of Alaska and Yukon there is abundant representation of fossil animals of Pleistocene time (see Gilmore, 1908; Quackenbush, 1909); it seems a fair assumption that conditions favorable for animal and plant life prevailed inland a little farther north when the whole coastal region was still buried under glacial ice.

The Sitkan district is characterized by heavy rainfall and relatively mild temperatures. It includes some of the wettest parts of the northwestern rain belt, with annual average precipitation of from 75 to 200 inches, perhaps more. "The temperature throughout southeastern Alaska is remarkably equable. The extremes recorded at Sitka show for August, the hottest month, an extreme range of from 35° to 87° F., and for the coldest month, February, a range of from 3° to 54° F. The mean temperature for January is 33°, and for August 56°, a range of only 23°" (Brooks and Abbe, 1906, p. 144). Mainland stations have more severe winter weather, with the mean annual temperature several degrees lower, and the inland fiords are decidedly colder than the outer coast line.

This is a region of dense vegetation, though with a limited variety of trees. Dense forest grows everywhere from the high-tide line upward to timber line. The dominant trees are the Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*), and there are lesser proportions of mountain hemlock (*Tsuga mertensiana*), western red cedar (*Thuja plicata*) and yellow cedar (*Chamaecyparis nootkatensis*). A few jack pine (*Pinus contorta*), small and twisted, grow in the bogs. Along the beaches, bordering the forest, there is nearly everywhere a line of alders (*Alnus sinuata*), and in places extensive thickets of willow, salmon-berry and devil's-club. There are small areas of grass-land where occasional high tides reach, and some open country (often snow or ice covered) on the higher summits of the islands.

The mainland strip of the Sitkan district is extremely narrow, the slopes of the Coast Range rising abruptly from the water's edge. The adjacent Alexander Archipelago comprises a multitude of islands with an intricate system of intervening channels. These waterways, some that are miles in width, others only a few yards across, are mostly protected from the swell of the open sea, but they are traversed by prodigious tides, in some places rising and falling twenty or thirty feet.

So, to summarize, the Sitkan district is a region of equable and rather cool temperature, of cloudy skies and heavy rainfall; densely covered with well-nigh impenetrable forest; a mass of mountainous islands mostly, separated by tide-swept channels; and offering a decidedly limited variety of surroundings to any potential fauna.

East of the separating Coast Range, less than one hundred miles inland, lies the interior of British Columbia, the western border of subarctic Canada, presenting sharp contrast to the coast in many respects, markedly so in the animal and plant life. This is a country of broad valleys, of lesser and scattered mountains and hills, of magnificent lakes and broad rivers. The valley floor at Atlin is at about 2,200 feet altitude, at Telegraph Creek 540 feet, and at Hazelton about 1,000 feet. There is here an abrupt falling off in amount of rainfall, Carcross, Atlin and Telegraph Creek having each an annual precipitation of from twelve to fifteen inches. At Hazelton, in the upper Skeena Valley, it is considerably more. Winters are severely cold, summers much warmer than on the coast. The inland woods, mostly rather open, are of different species from the coastal forests. The quaking aspen (*Populus tremuloides*) covers much of the lowlands, with balm of Gilead and birch in lesser abundance. White spruce (*Picea canadensis*) in the north, Engelmann spruce (*P. engelmanni*) farther south, are dominant lowland conifers, while alpine balsam (*Abies lasiocarpa*) grows on the heights, in prostrate form at its upper limit.

Between the Canadian interior and the Alaskan coast is interposed the formidable barrier of the Coast Range, a mountain chain about 60 or 70 miles through, both slopes rising abruptly, in places to 8,000 or 9,000 feet above the sea. These mountains are a barrier of absolute effectiveness as regards most animal species, in the climatic conditions induced on either side, in their rugged character and in the enormous areas that are still glacier-covered; and in the fact that the few openings through the range are densely covered with forest that is unattractive and inhospitable to nearly all birds and mammals. In the valley of the lower Stikine, one of the most important of the passes, there is heavy winter snowfall that is very slow to melt. The advent of spring is weeks later there than in the country on either side of the mountains, and this is an important factor in the delimitation of bird species which have to make the most of a brief summer.

There are a few channels of communication between the coast and the interior, offering varying degrees of accessibility. There are at the northern end of the Sitkan district the passes leading down to the head of Lynn Canal. About one hundred miles to the southward, near Juneau, is the valley of the Taku River, and one hundred and fifty miles farther, the valley of the Stikine, both important channels through the Coast Range. One hundred and fifty miles farther, at the southern boundary of Alaska, is Portland Canal, extending far inland, and just beyond, the Skeena River. This river

flows through a broad valley, piercing the Coast Range at a point where the mountains are of lesser height than farther north, thus permitting a more free intermingling of coastal and interior elements than elsewhere. Coastal rains and fog drift farther inland, and are accompanied by coastal species to some extent, and, on the other hand, certain influences from the interior have markedly affected the coastal fauna.

Compared with the coastal strip to the southward, the Sitkan region is of appreciably colder temperatures and of greater humidity, the variation in both respects southward into California being of gradual accomplishment. Compared with the adjacent interior east of the Coast Range, the Sitkan region is of a more equable climate with much milder winters, and it is of enormously greater humidity, these changes being accomplished most abruptly, within a distance of forty or fifty miles.

Along the entire coast, from Lynn Canal to Puget Sound, close restriction of the powerful coastal influences at the east is an important factor, of course, in the distribution of animal life; and it must be borne in mind as of no less importance in a discussion of possible routes to be followed by immigrant species from other parts. North-bound invaders that were sensitively adapted to coastal conditions have had an extremely narrow margin along which to travel. A slight mechanical obstacle on the coast became impassable when flanked by adverse climatic conditions so short a distance inland.

The retreating glaciers still linger on the mainland mountains of southeastern Alaska, where even now they cover hundreds of square miles. Disintegration travelled from west to east; clearly the islands were first to be free of the ice covering. On the whole Pacific coast from Puget Sound northward there is a bordering fringe of islands. First is Vancouver Island, slightly separated from the mainland, then along the British Columbia coast a narrow line of small islands lying close along the coast and the Queen Charlotte Islands farther out. From Dixon Entrance northward the Alexander Archipelago abruptly attains a width of one hundred miles or more, but with no very broad separating channels. That group of islands and perhaps some of those to the southward, together with the more remote Queen Charlotte Islands, must have been cleared of most of their glacial covering when the adjacent mainland still presented a wall of ice along its entire shore line. Birds with their powers of flight could advance quickly and freely northward from island to island; terrestrial mammals were shut off to the southward for a much longer period, until the slowly retreating glaciers began to leave a passage, narrow and interrupted to this day, along the mainland coast. So that the colonization of the Sitkan district by bird species from the southward, to the exclusion of most mammals, is perfectly comprehensible. The region, too, must for a long time later have been so

completely isolated from any eastern approach that the absence of birds from that direction can also be understood.

In a later period channels of communication above described were opened between coast and interior, north and east, through which various mammals passed, to compose the scanty mammal fauna that slowly and painfully progressed over varying parts of the Alexander Archipelago. The sifting through of these relatively few species must have been a long slow process. At a much later time an occasional bird species followed. This sort of colonization of both birds and mammals seems to me to be discernibly proceeding at the present time. As to the mechanics that controlled the actual planting of mammal species here and there, the imagination that would reconstruct past events will find stimulus in the vast surviving Alaskan ice fields, spanning the Coast Range as they do, and with raw traces of former activities spread out before their retreating fronts. At that, however, it might well be that actual sight of the continental ice sheets of Greenland or Antarctica is required to enable one to form a mental picture of what may have taken place in the northwest. This vision would paint a bleak unending ice field bordering salt water, broken only by small nunataks near the sea, by larger masses of rock, the Coast Range summits, farther back, an icy world that remained unchanged for ages. At last there transpired the gradual emergence of a rocky western coast line, of western islands, of channels that are sometimes distinguishable as such but still for ages longer clogged or hidden by bergs and other glacial debris swept down from mainland centers. Favored mainland sections, ice-free at last and eventually reached by mammalian life, could then have contributed a representation of species small enough to be borne to the islands upon such flotsam as the bergs might carry, or as today is brought down the large rivers and tossed upon island shores. Aquatic and semi-aquatic species would find opportunities for dispersal or have such thrust upon them. It would be a long slow process, slower than one can well realize, of the chance extension of a species from one island to the next, of the successive colonization of nunataks not yet recognizable as islands, all modified by glacial advances and recessions, and in the midst of tossing ice fields that must have been hurled in solid masses up and down the tide-swept channels long after the period when the glaciers, as such, ceased to fill these submerged valleys.

Along the mainland coast as far south as Puget Sound the retreating ice-front would release segments of coast, each bounded north and south by deep fiords or valleys still filled with ice. With the separated glaciers dwindled or vanished at the heads of these long valleys, paths were opened toward the coast for the westward advance of scattered inland colonies of various species of animals. These same narrow valleys, however, flooded with salt water sometimes twenty-five or thirty miles back from the general coast line, and extending inland to the limit of coastal influences or beyond,

although acting as highways from the east, formed a series of interruptions to the northward advance of any southern mammal that clung at all closely to the coast.

BIRDS

The birds of the Sitkan district form an assemblage that is separate and sharply distinct from that of the adjacent interior. There are very few species or subspecies that occur commonly in both sections. Birds and mammals of the Sitkan district have been regarded as possessing in common an extreme of dark brownish coloration, which is true to a certain extent but is not universal. This conception regarding the birds arose from the appearance of a group of fourteen or fifteen subspecies, the local representation of certain wide-spread and variable species, which occur in some abundance. Conspicuous among them are:

- Great Blue Heron (*Ardea herodias fannini*)
- Canada Goose (*Branta canadensis occidentalis*)
- Sooty Grouse (*Dendragapus fuliginosus sitkensis* and *Dendragapus fuliginosus fuliginosus*)
- Great Horned Owl (*Bubo virginianus saturatus*)
- Red-shafted Flicker (*Colaptes cafer cafer*)
- Steller's Jay (*Cyanocitta stelleri stelleri*)
- Oregon Junco (*Junco oreganus oreganus*)
- Song Sparrow (*Melospiza melodia rufina* and *Melospiza melodia morphna*)
- Fox Sparrow (*Passerella iliaca townsendi* and *Passerella iliaca fuliginosa*)
- Chestnut-backed Chickadee (*Penthestes rufescens rufescens*)
- Ruby-crowned Kinglet (*Regulus calendula grinnelli*)

There are additional species in which the "saturated" coloration is not so noticeable. They, with the previous list, all possess one common characteristic: residence the year through within the rain belt. Either they are permanently resident in the northern humid coast or else they perform a limited southward migration, perhaps as far as California, a migration that does not extend beyond the belt of heavy winter rainfall. Only resident forms have responded to local influences.

Here is a supplementary list representative of another set of breeding birds of the Sitkan district:

- Western Flycatcher (*Empidonax difficilis difficilis*)
- Lutescent Warbler (*Vermivora celata lutescens*)
- Townsend's Warbler (*Dendroica townsendi*)
- Pileolated Warbler (*Wilsonia pusilla pileolata*)
- Russet-backed Thrush (*Hylocichla ustulata ustulata*)

These, in contrast to the first lot, perform distant migrations, mostly into Mexico and beyond, and, breeding from southern Cali-

fornia to Alaska, they remain essentially unchanged throughout this habitat. They have not been affected by the stimulus that has darkened the resident species.

A third list:

Mallard (*Anas platyrhynchos*)
Spotted Sandpiper (*Actitis macularia*)
Greater Yellow-legs (*Totanus melanoleucus*)
Sharp-shinned Hawk (*Accipiter velox*)
Pine Siskin (*Spinus pinus pinus*)
Barn Swallow (*Hirundo erythrogaster*)
Tree Swallow (*Iridoprocne bicolor*)
Dipper (*Cinclus mexicanus unicolor*)
Western Golden-crowned Kinglet (*Regulus satrapa olivaceus*)

This is a selection of birds, wide-spread across North America or in the western half, some of them extensively migratory, two, at least (Dipper and Mallard), permanently resident, but all rather resistant, non-variable species, and none of them showing response in color to the influence of the humid coast.

Fair comparison can be made between the Canada Goose and Mallard, between Great Blue Heron and Spotted Sandpiper, between Song Sparrow and Pine Siskin. The Goose, Heron and Song Sparrow produce local races in other parts of their respective habitats, as in the Sitkan district; Mallard, Spotted Sandpiper and Pine Siskin are elsewhere indifferent to varied climatic surroundings, and have not altered perceptibly in the coastal environment. It is only notably plastic forms that have had time to respond to local influences.

Thus the strongly marked subspecies that are accepted as characteristic of the Sitkan district are, firstly, resident therein or within the slightly broader limits of the humid coast belt; and, secondly, they are races only of species whose external appearance varies so in different parts of their ranges as to suggest that slight influences and relatively short time are required to bring about such changes.

The Sitkan avifauna is composed mostly of species that are of southern derivation, northern offshoots of birds that are rather exclusively western or belonging to the still more limited Pacific slope. Among the few northern birds of permanent establishment and in fair abundance are the Willow Ptarmigan (*Lagopus lagopus alexandrae*) and Rock Ptarmigan (*Lagopus rupestris dixonii*), the former at high altitudes on all the larger islands, the latter on the more northern ones. The Pine Grosbeak, too, belongs in the category of northern immigrants. Clearly, though, it was the bird species from the south—and west of the southern Coast Ranges—that had first access to the region, pushing northward as conditions permitted, always west of the mountains.

In the Sooty Grouse, in the Fox Sparrows, and in the Song Sparrows there are well-defined subspecies occupying western and eastern portions of the Sitkan region. In the Grouse and Fox Sparrows one

form occupies the Alexander Archipelago and the Queen Charlotte Islands, another the mainland coast. In the Song Sparrow one form occupies the westernmost islands of the Archipelago and the Queen Charlotte Islands, another the inner islands and the mainland coast. This carries the suggestion that as the westernmost part of the region became free of ice, the first section to be habitable, it was at once occupied by these species; and these western colonies now show their greater age in their differentiation from the mainland stock.

At a much later period there began to be an occasional invader from the east, struggling through the few difficult passes from the interior, a movement that can be discerned today at such places as the mouths of the Skeena, Stikine and Taku rivers. At such spots there have been found small colonies or single birds of the following inland forms (see Swarth, 1911):

- Olive-sided Flycatcher (*Nuttallornis borealis*)
- Western Wood Pewee (*Myiochanes richardsonii richardsonii*)
- Alder Flycatcher (*Empidonax traillii traillii*)
- Louisiana Tanager (*Piranga ludoviciana*)
- Cedar Waxwing (*Bombycilla cedrorum*)
- Western Yellow-throat (*Geothlypis trichas occidentalis*)
- Tolmie Warbler (*Oporornis tolmiei*)

These are species that have barely secured a foothold on the coast, but some of them, at least, do breed there in small numbers without reaching the islands beyond. At some distant period the Hairy Woodpecker (*Dryobates villosus*) arrived through these channels and occupied the whole region, long enough ago to have since developed as a distinguishable subspecies, *D. v. sitkensis*. This form seems clearly to be an offshoot of the same white-breasted inland strain as *D. v. septentrionalis* of the Yukon region, and *D. v. monticola* of interior British Columbia, and not of the dark-breasted strain (*D. v. harrisi*) of the southern coast of British Columbia, as was formerly assumed. The Downy Woodpecker (*Dryobates pubescens leucurus*) and the Three-toed Woodpecker (*Picoides tridactylus fasciatus*) also reach the coast as migrants or occasional visitants, but have hardly established residence there. Another inland bird, Franklin's Grouse (*Canachites franklini*), unchanged, occupies some of the southern islands.

It is the species of southern derivation that have developed the striking local subspecies. The more recent arrivals from the east, even the sedentary Franklin's Grouse, have mostly not changed; the Hairy Woodpecker is one that has altered perceptibly. Of Sitkan subspecies that can be regarded as invaders from the north, such as Alexander's Willow Ptarmigan, Kodiak Pine Grosbeak, and Hepburn's Rosy Finch, all occupy additional territory too far to the northwest for these races to be considered as local products of the Sitkan district.

The broad valley of the Skeena forms a medium of communication between interior and coast that has had marked local results. Some species, such as the coastal Song Sparrow and Red-breasted Sapsucker, press far inland, meeting with no closely related form. The Yellow-shafted Flicker of the interior and the Red-shafted Flicker of the coast meet, with the result that the entire Flicker population 200 miles inland is strongly tinged with characteristics of the coastal species; hybrids also occur in the red-shafted population of the Alaska coast near the mouth of the Skeena. Franklin's Grouse must have reached the southern Alaskan islands through the avenue provided along the Skeena.

Local variation in Steller's Jay (*Cyanocitta stelleri*) hereabout leads to certain deductions that are at least worth stating. This species appears to be of far southern origin, extending from the highlands of Central America northward. There are two divergent strains, one in the Rocky Mountain region characterized by white markings on the eyelids, the other on the Pacific slope lacking these markings. At the southern limit of the last mentioned the two strains are separated by some hundreds of miles occupied by neither form, and there is no intergrading there. At the north, in the lower Skeena, the two strains are joined, and birds with the head markings of the interior Black-headed Jay (*Cyanocitta stelleri annectens*) occur upon the coast in the ascribed range of Steller's Jay (*C. s. stelleri*). There is apparently true intergradation here between the two subspecies, such as I believe does not exist elsewhere between these two strains. Along the coast north of the Skeena and south of the Skeena "typical" *stelleri* occurs. Opposite the mouth of the Skeena, on the Queen Charlotte Islands, is the still more heavily "saturated" subspecies, *C. s. carlottae*. The point to be emphasized is that where *stelleri* and *annectens* meet intergradation, that is, merging of characters, actually occurs. The significance of this fact becomes apparent when we consider that in the case of almost every other variable species in this region with separate inland and coastal subspecies, wherever they meet—and many of them do meet—they come together as distinct species, either not interbreeding at all or else producing occasional hybrids. I have come to the belief that these meetings are between strains that have long been separated, extending northward along separated routes and eventually coming together at too late a period to permit intermixture; though, perhaps, in the far south the representatives of the same two strains might never have broken entirely apart. By this theory the two strains of *Cyanocitta stelleri* did not meet in this northern region—on the contrary, this was the point of separation. It looks to me as though the Jays of this species (*Cyanocitta stelleri*) might have emigrated northward and westward along the Rockies, reached their present northwestern limit in the Skeena drainage, arrived thereby to the coast, and from this base or thereabout, spread northward and southward over their present-day habitat on the Pacific slope.

There are bird species of circumpolar distribution with widespread representation in the New World as in the Old, that in both regions moved from the north southward to occupy their present habitats. Of this category the Willow and Rock ptarmigans were apparently early and direct immigrants into the Sitkan district, but with these exceptions and one or two others the southbound northerners were deflected to the eastward, away from the coast. The American Three-toed Woodpecker is one that at a later period made an indirect approach from the eastward when opportunity offered, exemplifying a colonization scheme that is still in its early stages. Magpie, Bohemian Waxwing, Common Redpoll and Northern Shrike are all species that were barred from the coast in the southern expansion of their habitats and are now found east of the Coast Range in association with southern species that were similarly barred in their northward migrations. The Pine Grosbeak of the Sitkan district is apparently the same subspecies (*Pinicola enucleator flammula*) as that of the Alaskan coast to the northwest, as far as Kodiak Island. From its extreme rarity it may be supposed to be a recent arrival from the northern part of its range; but in any event it is one of the very few coastal species that has penetrated eastward through the Coast Range. The coastal Pine Grosbeak occurs inland along the Stikine River as far as Telegraph Creek. Hepburn's Rosy Finch is another bird of northern derivation, and the Rusty Song Sparrow and Sooty Fox Sparrow are birds of southern origin, that have likewise extended their habitats inland as far as the eastern face of the Coast Range along the same river valley. These birds have all entered a region that is not otherwise occupied by the several genera to which they belong.

There are about twenty kinds of birds with complementary representation on the coast and inland, as subspecies or closely related species; in most cases there is no more intergradation exhibited between the subspecies than between the species. Exceptions are found in the subspecies of the Hairy Woodpecker, Steller's Jay, Lincoln's Sparrow and Yellow Warbler. As regards the Hairy Woodpecker and Steller's Jay, my conviction, as already explained, is that the coastal populations are directly derived from the interior stocks and that there has never been separation. The same is probably true of the coastal subspecies of Lincoln's Sparrow (Forbush's Sparrow) and of the Yellow Warbler (the Alaska Yellow Warbler). In both cases mode of occurrence upon the coast favors this view, and both are very faintly distinguished local forms, even in their extreme manifestations.

For the rest, the long list of species with comparable representation on the coast and inland includes such contrasting forms as Sooty Grouse and Richardson's Grouse, Western Red-tail and Harlan's Hawk, Red-shafted Flicker and Yellow-shafted Flicker, Oregon Junco and Slate-colored Junco, Chestnut-backed Chickadee and Hudsonian Chickadee, Russet-backed Thrush and Olive-backed

Thrush. In none of these cases are there found between contrasting forms any intergradient populations; the differences are all clean cut.

There is a long list of bird species of the interior that have no comparable representation on the coast. The list of Sitkan birds that have no representation east of the Coast Range includes characteristic coastal subspecies, common birds in the region mostly, of the following species: Canada Goose, Pine Grosbeak, Rosy Finch, Song Sparrow, Fox Sparrow, Winter Wren, Brown Creeper, Golden-crowned Kinglet, and Varied Thrush. These are all widely distributed species that occur north and south of this region. In some cases outlying colonies of one or another of these birds have advanced a short distance inland, but there is an enormous extent of northern British Columbia immediately east of the Coast Range that has none of these species represented in a breeding population.

MAMMALS

Of the mammals of the Sitkan district, those that clearly are directly derived from the north are found on the three large islands, Chichagof, Baranof and Admiralty, the northernmost of the archipelago and most easily accessible from the northern mainland. These species include the huge brown bears, at their southern limit upon these islands, and the Sitkan Meadow-mouse (*Microtus sitkensis*).

As regards the rest of the islands and the mainland, most of the smaller species arrived from the adjacent interior east of the Coast Range, their origin and their recent arrival being clearly shown in a great many cases by the mode of variation and by the local distribution of the species concerned. That the islands of the Alexander Archipelago were thus populated after their separation by the present network of channels may be inferred from the steady diminution in the numbers of species as one progresses westward from the mainland, island by island. At various mainland localities between Juneau and Dixon Entrance as many as twenty-four species of mammals may be expected to occur. Of certain large islands immediately adjoining the coast, there are thirteen species recorded from Admiralty, twelve from Kupreanof, and twelve from Revillagigedo. Going farther west, there are six from Coronation, five from Warren, and seven from Dall.

To take specific examples, the following species occur along the mainland coast but on none of the islands: Mountain Goat (*Oreamnos*), Stikine Jumping Mouse (*Zapus saltator*), a Red-backed Mouse (*Clethrionomys phaeus*), and a Marmot (*Marmota caligata*). Other common mainland forms reach one or two of the most accessible islands: Porcupine (*Erethizon dorsatum*) on Wrangell and Etolin; a Jumping Mouse (*Zapus hudsonius*) on Revillagigedo; Musk-rat

(*Ondatra zibethica spatulata*) on Revillagigedo and Sergief; a Red-backed Mouse (*Clethrionomys wrangeli*) on Revillagigedo and Wrangell; a Lemming Mouse (*Synaptomys dalli wrangeli*) on Wrangell; a Flying Squirrel (*Glaucomys sabrinus zaphaeus*) on Etolin, Wrangell and Prince of Wales.

The distribution of the Sitkan Red Squirrel (*Sciurus hudsonicus picatus*) seems to be plainly the result of the accessibility of certain islands from the mainland under present conditions. This squirrel occurs on all the inner line of southern islands that are so slightly separated from the coast, and it is also on certain islands (Mitkof, Kupreanof and Kuiu) that, extending to the western limits of the archipelago, form a series of easily traversed stepping stones from the coast. Osgood (1900, p. 28), in his description of the White Pass Red Squirrel, *Sciurus hudsonicus petulans*, remarks: "The closest relationship of this red squirrel is evidently with *hudsonicus* of northern Alaska. . . . There is ample material demonstrating by skulls as well as by color that it has no very close relationship to *S. vancouverensis*" (of Vancouver Island). *Petulans* is clearly an intermediate step between inland *hudsonicus* and Sitkan *picatus*.

The Timber Wolf is found upon the same islands as the Red Squirrel, and also upon the large Prince of Wales and Dall islands with some others of this southern group that the squirrel has never reached. Evidently the wolf did not come directly from the north. Island distribution of Timber Wolf and Black Bear is exactly the same. If the significance here is that these islands were equally accessible to both species, then the complementary distribution of Black Bear and Brown Bear in the archipelago, nowhere found both upon the same island, is no more than a coincidence.

The Meadow-mice excellently illustrate island distribution as determined by recent accessibility. (See map, fig. 1.) The Sitkan Meadow-mouse (*Microtus sitkensis*) is only on Chichagof and Baranof, and it is the only *Microtus* upon those islands. This is a southern offshoot of a group of mice (the *operarius* group) that occupies much of the Alaskan mainland to the northward. The islands where it is found are conceivably accessible from the northern mainland, surrounded by the open sea and mighty channels on other sides. The most common Meadow-mouse of the Sitkan district is *Microtus mordax littoralis*; this is a local race of *M. mordax*, which is of common and wide-spread occurrence east of the Coast Range. *Littoralis* has been found at some points on the mainland coast, and it occupies most of the islands, but not Chichagof and Baranof. The ancestral *mordax* may be assumed to have reached the coast from the adjacent interior at a very early period. It has been there long enough not only to have developed a recognizable local race of wide-spread distribution over the archipelago, but to have produced also the remarkable giant form, *Microtus coronarius*, that occupies certain of the small out-lying islands.



Fig. 1. Map showing distribution of *Microtus operarius* (A), *M. pennsylvanicus* (B), and *M. mordax* (C) in southeastern Alaska. Arrows indicate assumed lines of migration of the species. *Pennsylvanicus* and *mordax* occupy in company most of the adjacent interior of British Columbia, *operarius* most of Alaska; the map shows only such limited portions of the general ranges as contributed directly to colonization of the coast. Map drawn by Miss Margaret W. Wythe.

Drummond's Meadow-mouse (*Microtus pennsylvanicus drummondii*), abundant throughout the northwestern interior, has found its way through the Coast Range in at least two places, along the valleys of the Taku and Stikine rivers. Presumably it is of more recent arrival upon the coast than the predominant *littoralis*, for although there are colonies at the mouths of those streams the species has not spread farther on the mainland. It is noteworthy, however, that it did reach Admiralty Island, the northern end of which is directly opposite, and not very far removed from, the mouth of the

Taku. The island mouse has been given a name, *admiraltiae*, but it is very slightly different from the mainland *drummondi*.

There are two species of shrew that occur in abundance in the Sitkan district, the Masked Shrew (*Sorex cinereus*) and the Dusky Shrew (*Sorex obscurus*), each represented by local subspecies. The species *Sorex cinereus* is transcontinental in range, extending across northern North America. The species *Sorex obscurus* is western, found from the Rocky Mountains to the Pacific. I receive the impression that *obscurus* was the first arrival in the northwest, probably coming from the south. It is of more general distribution than the other, having reached even the westernmost of the islands of the Alexander Archipelago and also the Queen Charlotte Islands. *Cinereus* occurs on the large northern islands, Baranof, Chichagof and Admiralty, but in the south it has not got beyond the islands that immediately adjoin the mainland. Delimitation southward at Frederick Sound, westward at Clarence Strait, is suggestive of invasion from north and east. The coastal population of *Sorex cinereus* is comprised in just one subspecies, *S. c. streatoris*, and that one is but slightly differentiated from the inland parent stock. The Dusky Shrew (*Sorex obscurus*), besides attaining to every island, has been long enough resident to have evolved four recognizable subspecies, *S. o. alascensis* in the region about Juneau, *S. o. longicauda* on the mainland coast farther south, *S. o. elassodon* on most of the Alexander Archipelago and on the Queen Charlotte Islands, and *S. o. malitiosus* on the small islands, Coronation and Warren.

There are on the Alaskan coast small colonies of certain mammals, such as Marmot, Porcupine and Muskrat, that do not occur on the coast farther south. These obviously are derived from inland sources, and their presence affords evidence corroborative of the impression that many other components of the Sitkan mammal fauna came from the same direction. The one Sitkan mammal unmistakably of southern coastal origin is the Black-tailed Deer (*Odocoileus columbianus*). This is the only ungulate upon the islands, in contrast to conditions in the adjacent interior, where Moose, Caribou, Mountain Goat and Mountain Sheep abound. Rare upon the mainland, this deer is extremely abundant on all the Alaskan islands, where it reaches the northernmost point attained by the genus *Odocoileus*. It is equally abundant upon Vancouver Island, but the species never reached the Queen Charlotte Islands. The Dusky Shrew, previously mentioned, is the only other mammal of which there seems a fair likelihood of arrival from the south along the coast.

Among the mammals, as with the birds, there are well-defined forms that are restricted to the western islands, affording corroborative evidence of an earlier fauna existent in that part. The peculiar distribution of *Peromyscus sitkensis* and *Microtus coronarius* is certainly suggestive of these being representatives of a relict fauna.

In studying the origins of a given fauna some light may be obtained through considering species that might be expected to occur within the area but do not. In the present case there are excellent examples at hand. There are no rabbits in the humid northwest coast region—a remarkable fact. There are rabbits over most of the world, in as widely diversified surroundings as any form of animal life, and the rabbit meets these varied conditions with a minimum of structural change. Under the circumstances, the absence of these animals from the coastal forests would seem to be due to there not having been time since establishment of those forests for invaders from the abundant rabbit population of the adjacent interior to have acquired any slight adaptations necessary for existence on the coast; in other words, that the coastal area has been habitable for a relatively brief period.

There are no native cats in the northwest coast region. The Canada Lynx is of general distribution across subarctic North America eastward from the Coast Ranges. In the periods when the fluctuating rabbit population is at its height the Lynx, too, increases in numbers, and at such times occasional individuals wander to the coast, but otherwise the species is absent from the rain-belt. That the Lynx has failed to establish itself in the Sitkan district, despite sporadic visitations that prove the animal's ability to reach the place, might be ascribed to the absence of rabbits from that section, and of other suitable prey in sufficient quantity, but these apparent deficiencies do not supply a satisfactory explanation. It is a notable fact that the Puma has similarly failed to invade the Sitkan district from the south, under apparently favorable conditions. Deer, the usual prey of the Puma, extended their habitat northward and over the Sitkan islands as climatic conditions permitted, but the Puma, abundant on Vancouver Island, encountered some adverse influence north of that point that did not affect the Black-tailed Deer. This could not have been excessive rainfall alone, for there is not sufficient difference in this regard between the west coast of Vancouver Island and the Sitkan district. If the explanation lies in the difference in temperature, it bespeaks a notable lack of adaptability, that, in the period when the Deer was pressing northward, the Puma could not become accustomed to the relatively slight drop in temperature, even when supplied with an abundance of its accustomed food and under conditions where this food was singularly easy to secure. There is the suggestion here, in harmony with the general aspect of the Sitkan fauna, that the Alexander Archipelago acquired its deer population after the islands became water-girt, the intervening channels—no obstacle at all to deer—being barriers of absolute efficiency against Puma and Lynx. At any rate, the Sitkan district of Alaska and the British Columbia coast for a long distance south of Alaska, are uninhabited by any species of native cat. This is a deficiency to be pondered by those who believe that in the last

analysis the numbers of any species of animal are governed by the available supply of food.

There are other species, too, such as Muskrat, Porcupine and Red Fox, to name some of the most notable, whose slight establishment upon the Alaskan coast or entire absence therefrom seem best explained as due to the very recent accessibility of the region to those animals. Viewing the wide-spread and diversified habitats some of them already occupy, it is hard to believe in the presence of factors in the Sitkan surroundings that are sufficiently adverse to prohibit existence there. The scanty colonies here and there of one species or another are strongly suggestive of a slow advance, each along some favorable path, the several species being thrust forward to varying degrees in the partly occupied territory. Coast and interior are widely different in details of the plant assemblages, with different trees and different shrubs, but certain types of surroundings are closely duplicated in the two sections. There are forests, bogs, and open, timberless mountain tops among the various "habitats" of the two regions; and scanning the distribution of certain of the animals in question it is evident that acceptability of surroundings (the "ecological niche") is not necessarily determined elsewhere by the specific identity of the assembled plants. It is hard to believe that the Porcupine can thrive in white spruce forests but not in Sitka spruce. It is hard to believe that the presence of Franklin's Grouse in a restricted portion of the Sitkan district is due to anything but the accidental and recent accessibility of the occupied area from the main stronghold of the species east of the Coast Range.

AMPHIBIANS

The limited amphibian population of the Sitkan district includes two invaders from the south, a toad of common and wide-spread occurrence, a newt that is found on many of the southern islands; and one immigrant from the east, a frog that barely enters the district.

The Northern Toad (*Bufo boreas boreas*) is abundant on the coast as far north as Prince William Sound. It has attained this far northern point not only along the mainland coast but on the islands as well. It is on at least all the larger islands in Prince William Sound, those of the Alexander Archipelago, of the Queen Charlotte group, and on Vancouver Island. The wide-spread distribution of this toad is in strong contrast to the inability of any species of frog to become strongly established in the same region. The toad is a western species and may be surmised to have traveled northward along the coast. Just how it reached the many northern islands where it now occurs is not clear; the genus is not represented on any island south of the United States-Canada boundary line, though common enough on the adjacent mainland.

The Western Spotted Frog (*Rana pretiosa*) is the one species of frog that has reached the Sitkan district. It is a common species inland and it has extended its habitat the length of the Stikine River to Sergief Island, at the mouth of that stream. The salt water channels beyond are clearly formidable barriers to farther range extension, barriers that may never be passed; and the restriction of this frog emphasizes the query as to the means by which the toad achieved its present widespread distribution.

The Pacific Coast Newt (*Triturus torosus*) is a coastal species that finds its northern limit in the Sitkan district and that probably reached this region in the same manner as, and together with, the Northern Toad. It has been found on enough of the islands of the Alexander Archipelago to make it seem likely that it occurs throughout the group.

SUMMARY

The facts that we have marshalled lead to the following conclusions: The fauna and flora of the Sitkan district are of recent establishment there; probably none of the island area was free of ice and occupied by any of this animal and plant life prior to the close of Pleistocene time, and large sections may have become habitable only at a much later date. Local specific or subspecific characters in birds and mammals thus may all have developed since the Pleistocene. The bird species are mostly derived from the coastal region to the southward; these southern species were the first arrivals and have spread over most of the district. A few kinds came in from the north; a few kinds came through mountain passes and valleys from the east, and these are mostly of limited distribution in the eastern portion of the Sitkan district.

Conditions that permitted the spread of birds from the south were unfavorable to most mammals. One southern mammal, the deer, was conspicuously successful in this immigration, and there may have been one or two others, but most of the mammals of the Sitkan district are from the east, whence approach by birds was apparently more difficult. Several northern mammals colonized certain northern islands of the Alexander Archipelago that were most easily accessible from that direction.

The distribution of species over the Alexander Archipelago is to be explained mainly on the basis of the present accessibility of the islands. There is the added suggestion in the observed development of certain species and subspecies (as the Song Sparrow), that the westernmost islands, first to be cleared of their glacial covering, may have been first to be occupied by living things. Depth and width of the separating channels, however, were determined long before, so that with the disappearance of glacial ice, and with the arrival of animal life, these barriers were all functioning as they do today.

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